RESEARCH ARTICLE

Interaction of traffic intensity and habitat features shape invasion dynamics of an invasive alien species (*Ambrosia artemisiifolia*) in a regional road network

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Abstract

Road corridors are important conduits for plant invasions, and an understanding of the underlying mechanisms is necessary for efficient management of invasive alien species in road networks. Previous studies identified road type with different traffic volumes as a key driver of seed dispersal and abundance of alien plants along roads. However, how the intensity of traffic interacts with the habitat features of roadsides in shaping invasion processes is not sufficiently understood. To elucidate these interactions, we analyzed the population dynamics of common ragweed (*Ambrosia artemisiifolia* L.), a common non-indigenous annual species in Europe and other continents, in a regional road network in Germany. Over a period of five years, we recorded plant densities at roadsides along four types of road corridors, subject to different intensities of traffic, and with a total length of about 300 km. We also classified roadsides in regard to habitat features (disturbance, shade). This allowed us to determine corridor- and habitat-specific mean population growth rates and spatial-temporal shifts in roadside plant abundances at the regional scale. Our results show that both traffic intensity and roadside habitat features significantly affect the population dynamics of ragweed. The combination of high traffic intensity and high disturbance intensity led to the highest mean population growth whereas population growth in less suitable habitats (e.g. shaded roadsides) declined with decreasing traffic intensity. We conclude that high traffic facilitates ragweed invasion along roads, likely due to continued seed dispersal, and can compensate partly for less suitable habitat features (i.e. shade) that decrease population growth along less trafficked roads. As a practical implication,

management efforts to decline ragweed invasions within road networks (e.g. by repeated mowing) should be prioritized along high trafficked roads, and roadside with disturbed, open habitats should be reduced as far as possible, e.g. by establishing grassland from the regional species pool.

Introduction

Plant invasions are a global phenomenon closely linked to human activities and related transportation network infrastructures (Bradley et al. 2012; Seebens et al. 2015; Chapman et al. 2017). A large number of studies revealed the importance of road corridors for the spread of invasive plant species (e.g. von der Lippe and Kowarik 2007; Brisson et al. 2010; Joly et al. 2011; Dar et al. 2015; Manee et al. 2015; Okimura et al. 2016; Follak et al. 2018a) and identified several important anthropogenic dispersal vectors as reviewed by Ansong and Pickering (2013). These vectors are commonly related to construction work, road maintenance and roadside management, agriculture, transportation industry and private vehicles. Depending on factors like vector velocity (Taylor et al. 2012), seed accrual rate (Rew et al. 2018) and seed adhesion time (Bajwa et al. 2018) the achieved dispersal distances can range from some tens of meters to hundreds of kilometers for road vehicles (von der Lippe and Kowarik 2007; Taylor et al. 2012; Lemke et al. 2019). An estimation from experimental data on dispersal by adhesion to vehicles revealed that approximately every hundredth seed transported by road vehicle is likely to be dispersed more than 5 km in road networks (Taylor et al. 2012). As regional dispersal corridors, roads therefore probably play an important role for plant invasions (Vicente et al. 2014). Observed distribution patterns of alien plant species in road networks suggest traffic volume as one key variable related to the dispersal process (Vakhlamova et al. 2016; Barlow et al. 2017; Geng et al. 2017; Horvitz et al. 2017). At a local scale, traffic intensity is known to affect the diversity and composition of roadside vegetation (Truscott et al. 2005; Jaźwa et al. 2016), and distribution patterns of invasive alien species as well (Lemke et al. 2019).

Traffic volume has also been shown to trigger abiotic parameters like pollutant load (e.g. Jantunen et al. 2006; Neher et al. 2013; Mikołajczak et al. 2017) or the level of physical disturbance on road verges (Truscott et al. 2005; Johnson et al. 2006). Compared to the surrounding habitats, roadsides are physically, chemically and biologically altered environments (Forman and Alexander 1998) receiving more light, additional moisture from road drainage and sometimes additional mineral nutrition from adjacent agricultural fields. As a negative effect in this habitat, plants are stressed by pollutants from traffic exhausts and by de-icing salt that also affects soil pH (Forman and Alexander 1998; Seiler 2000; Hofman et al. 2012; Gentili et al. 2017). Habitat quality of roadsides is locally modulated by adjacent land- use patterns that may result in differences in shading or disturbance intensity (Christen and Matlack 2009; Speziale et al. 2018). We expect that both shading and the availability of open habitats at road

verges are critical for the establishment of roadside populations because most plant species growing on roadsides are commonly categorized as herbaceous generalists (Coffin 2007) or light, drought and disturbance tolerating ruderal specialists (Sera 2010; Gade 2013; Bochet and Garcia-Fayos 2015; Kalwij et al. 2015).

While several vectors of human-mediated dispersal at roadsides are well understood, their effects on regional population dynamics of alien plants along roads and their interplay with habitat quality and adjacent land use have hardly been studied. A better understanding of interactions between traffic-related and habitat-related drivers of plant invasions along roads would also support the early detection of alien species, their control and related management measures – if necessary – in management at local or regional scales (Cabra-Rivas et al. 2015; Lembrechts et al. 2017).

We use *Ambrosia artemisiifolia* L. (henceforth common ragweed) as a model species to elucidate relationships between traffic- and habitat-related features of road corridors. Common ragweed is an annual ruderal plant species that is well adapted to roadside habitats (Essl et al. 2015). Seedling recruitment is highly increased by frequent disturbance of these sites and specimens can reach large biomass (Fumanal et al. 2008; MacDonald and Kotanen 2010). Common ragweed develops best under full light conditions but tolerates lower light conditions, yet with reduced fitness (Montagnani et al. 2017). Understanding invasions by common ragweed is important, since this species severely affects human health by allergenic pollen; it is also an important agricultural weed (Bullock et al. 2012; Essl et al. 2015; Sölter et al. 2016).

The spread of common ragweed is limited by low natural dispersal rates (barochory; Essl et al. 2015; Lemke et al. 2019) and a reduced plant growth at deeply shaded habitats (e.g. forest understoreys; Joly et al. 2011; Qin et al. 2012). While natural dispersal rates cannot explain the rapid range expansion of common ragweed throughout Europe (Essl et al. 2009; Ozaslan et al. 2016; Skalova et al. 2017), there is growing evidence about the different human-mediated dispersal processes that support its invasion success. First introduction and repeated new invasion foci resulted mainly from contaminated seed lots of grain, oil seed or bird food (Montagnani et al. 2017). Several modes of dispersal related to traffic corridors have been shown to transport relevant numbers of seeds, sometimes over long distances, e.g. soil movement for construction purposes (Brandes and Nitzsche 2006), adhesion and loss of diaspores from mowing machinery (Vitalos and Karrer 2009), seed losses from trucks that carry contaminated grain or soil (Nawrath and Alberternst 2010) and finally direct dispersal by the slipstream behind vehicles and adhesion to tires (von der Lippe et al. 2013; Lemke et al. 2019) as a common and predictable process at the local scale. While there is increasing information and experimental evidence about these dispersal vectors, the interacting effects of traffic and site conditions on the spread of common ragweed on a regional scale are still poorly understood. In this study, we address the population dynamics of common ragweed on a regional scale by performing a road-network analysis to reveal the spatial-temporal dynamics in roadside populations of common ragweed. We systematically compare plant abundances between different road corridor types over a period of years and evaluate the contribution of traffic density and habitat type, and their interactions, on the dynamics of these roadside populations.

Based on our multi-annual approach we test the following hypotheses: (a) traffic intensity affects the expansion and densification of common ragweed populations along roads, resulting in growth rates linked to the corridor type (from high to low traffic intensity); (b) habitat type affects the population growth of common ragweed resulting in higher plant densities on disturbed roadsides compared to undisturbed roadsides and lower plant densities for shaded compared to un-shaded habitats; and (c) depending on the corridor type, the interaction between traffic- and habitat-related factors leads to changes in population growth in similar habitat types.

Material and Methods

Study species

Common ragweed (*Ambrosia artemisiifolia* L.) was chosen as a model species because its spatial distribution patterns are closely related to human activities – especially to transportation corridors, with rail or road traffic likely functioning as major dispersal vectors (Bullock et al. 2012). The species is native to parts of the United States and southern Canada and has spread to several parts of the world (Makra et al. 2015; CABI 2016). It was introduced to Europe in the 19th century and is now naturalized in several countries (Montagnani et al. 2017). Its allergic pollen affects public health in several European countries where it is most abundant in southeast Central Europe, north Italy and southeast France (Smith et al. 2013; Lake et al. 2017; Rasmussen et al. 2017). Preventive management is also needed for less invaded countries like Germany to reduce future health costs (Born et al. 2012). In consequence, management efforts target common ragweed, both nationally and internationally (Bullock et al. 2012; Sölter et al. 2016).

Common ragweed grows in a range of open and disturbed habitats like wastelands, old fields or agricultural areas and along transportations corridors (Essl et al. 2015). While its natural dispersal is limited to distances around 1 meter (Lemke et al. 2019), the rapid spread of common ragweed in its introduced range can be explained by several human-mediated dispersal vectors both in Europe (Essl et al. 2015) and in North America (Joly et al. 2011). Seeds of common ragweed are mainly dispersed unintentionally with the transport of contaminated commodities like sunflower seed, soil movements and traffic or roadside management (Vitalos and Karrer 2009; von der Lippe et al. 2013; Lemke et al. 2019). Before it was regulated in the EU, contaminated birdfeed was a major pathway for repeated introductions (Bullock et al. 2012).

Study region

The study region (35 km × 35 km; road network of 300 km) is embedded in the historical region of *Niederlausitz* (Federal State of Brandenburg, Germany) and one of the hotspots of common ragweed in Germany (Buters et al. 2015). This area includes
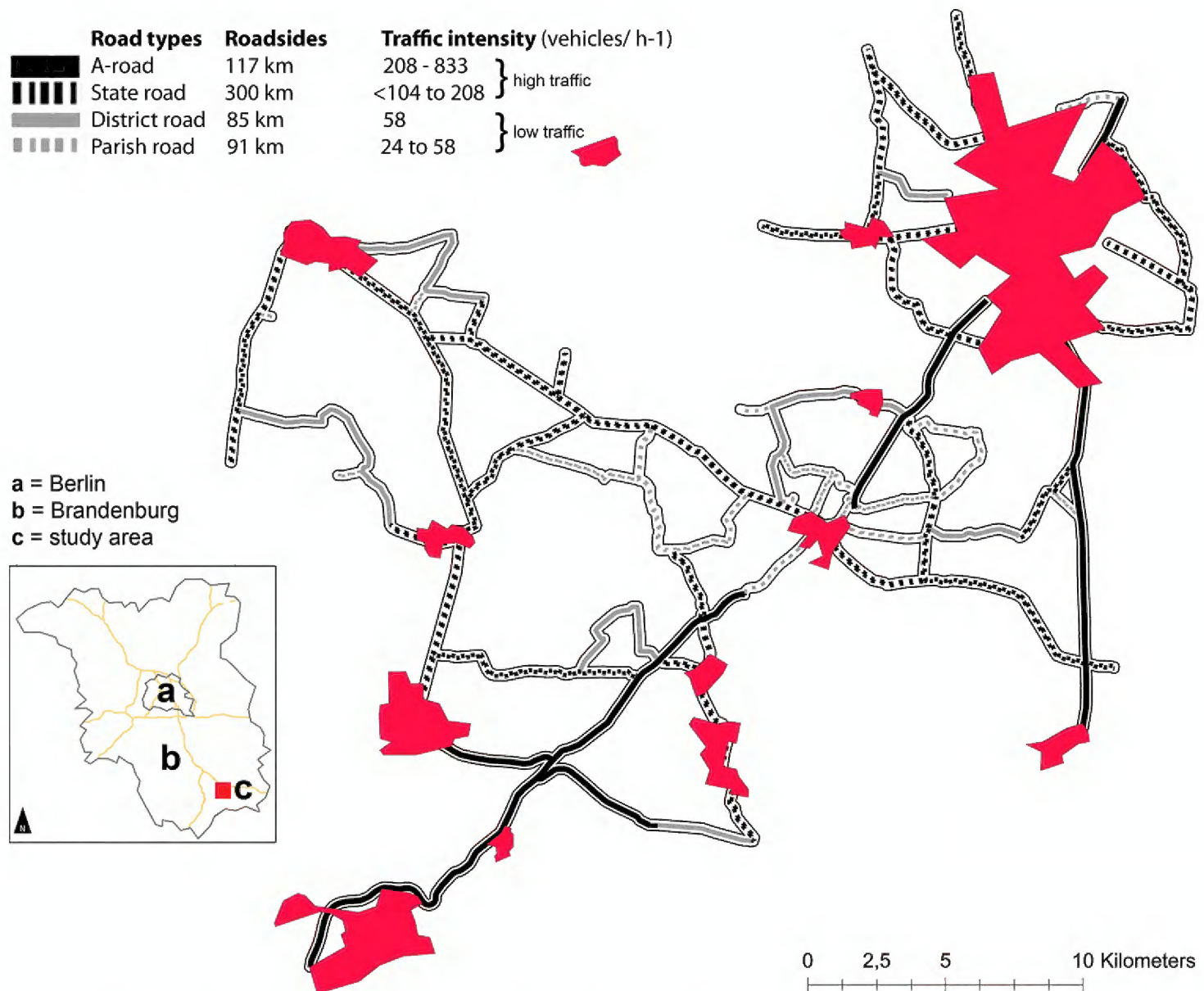
Figure 1. The study area (**c**) is situated in the south east of the Federal State of Brandenburg, Germany (**b**). The mapped road network consists of four road types (black line: *a-road*, black dotted line: *state road*; grey line: *district road*; grey dotted line: *parish road*). Based on official and additional vehicle counts we pooled a-road and state road to *high traffic intensity roads* and district road and parish road to *low traffic intensity roads*. Settlements are displayed in red.

many populations along the local road network and on adjacent agricultural and rural sites (Brandes and Nitzsche 2007) where the species has been observed as an agricultural weed since the 1970s (pers. com. staff members of Agrargenossenschaft Drebkau, 2010). A first systematic absence-presence mapping of common ragweed in the region of Cottbus-Drebkau-Calau revealed that about half of the mapped roadsides (60 km of 125 km) were colonized, yet with different occupancy patterns in the two years of the census (Nitzsche 2010). Starfinger (2008) also reported a high number of linearly spaced roadside populations in this region, mostly consisting of small plants of about 20 cm in height. Lemke et al. (2019) found that most of the plants grow in the first 0.5 m to the road border.

Within the road network analyzed in this study (Fig. 1), local road maintenance staff mowed all roadsides twice a year, independently of the traffic intensity of the road corridor, with a first service in June and a second service in autumn (September to
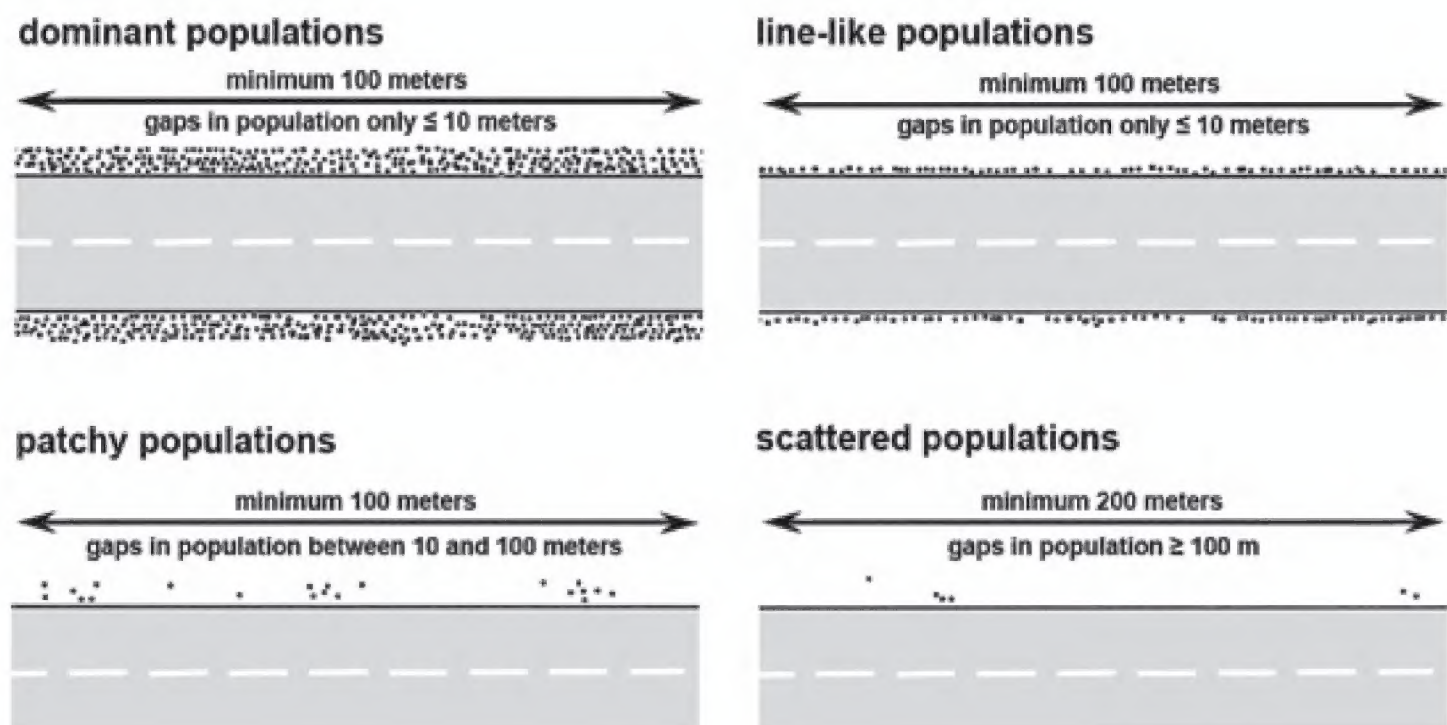
dominant populations

minimum 100 meters

gaps in population only ≤ 10 meters

line-like populations

minimum 100 meters

gaps in population only ≤ 10 meters

patchy populations

minimum 100 meters

gaps in population between 10 and 100 meters

scattered populations

minimum 200 meters

gaps in population ≥ 100 m

Figure 2. Visualization of the four population density classes of common ragweed mapped in the road network survey. Note that the minimum length for a change in recorded plant density during the mapping was different for 'scattered populations' (200 m) compared to the other three density classes (100 m). Dominant populations differed from line-like populations in their lateral expansion perpendicular to the roadway.

October). Staff members were aware of the presence of this plant in the road network (pers. com. road maintenance staff, 2009 and 2012). During the survey, we did not notice any adjustment of management (e.g. frequency or timing of mowing) for the different corridor types or population densities of common ragweed.

Roadside survey

Our field survey included five semi-quantitative mappings of common ragweed roadside populations in the years 2008 to 2012. In each of these five years, we conducted a census in summer (July to August) when common ragweed was best visible along the roads and easy to distinguish from the other roadside vegetation by its characteristic greenish color. The total length of mapped roadsides was about 300 km. We classified four plant density categories of common ragweed (Fig. 2) to evaluate population dynamics between the respective years. For each census we mapped the roadsides visually from a slowly moving car (Starfinger 2008) and captured the density categories of common ragweed plants as well as related adjacent landmarks like field entries or forest borders to precisely locate the mapped common ragweed patches.

We classified four road types according to traffic volume (Fig. 1), based on existing data for a-roads and state roads (Landesbetrieb Straßenwesen Brandenburg 2010) and on personal vehicle counts along district roads and parish roads 2008 (Lemke, unpublished). For an overall measure of traffic intensity, we merged a-roads (208 to 833 vehicles/h) and state roads (<104 to 208 vehicles/h) to roads with high traffic volume because for both road categories the official vehicle count was beyond our 'medium traffic' threshold (58 vehicles/h; see Lemke et al. 2019). Likewise, we combined district

roads and parish roads to roads with low traffic volume (24 to 58 vehicles and <24 vehicles, respectively).

In 2012, we conducted an additional roadside habitat mapping from a slowly moving car to capture habitat features that we expected to potentially limit ragweed populations in road corridors. The underlying classification of roadside habitats was chosen after a thorough inspection of the different characteristics of roadsides in the field. First, we differentiated shaded from un-shaded (i.e. sunny) habitats. We assigned all roadsides to the category "shaded" that were shaded most of the day by close tree lines, tree stretches or single trees, or by an adjacent forest canopy, given that all of these elements clearly reduce light availability on the ground – which we hypothesized to limit common ragweed establishment. Since we expected a dense vegetation cover to limit the population establishment of common ragweed as well, we further differentiated the sunny roadside sections into disturbed and undisturbed sections according to a vegetation cover of <50% and of >50%, respectively, assuming that most kinds of disturbance lead to open soil patches along roads. We were not able to differentiate the shaded roadsides into disturbed and undisturbed sections as these sections were generally characterized by a sparse vegetation layer that made it impossible to visually distinguish disturbances from the slowly mowing car. However, we argue that in this habitat type recruitment is limited by shade rather than by the limitation of safe sites as the share of open soil was high throughout the road network. This classification resulted in three well distinguishable habitat types with recurring vegetation elements. The **undisturbed roadsides** frequently contained species of ruderal grasslands like *Poa pratensis*, *Lolium perenne*, *Bromus hordeaceus*, *Achillea millefolium* or *Rumex crispus*. In **disturbed roadsides**, these species gradually drop out and typical disturbance indicators appear such as *Poa annua*, *Stellaria media*, *Conyza canadensis* and *Matricaria discoidea*. Along the **shaded roadsides**, some of the competitive grassland species of the undisturbed sections still occur, supplemented by some species of shade-tolerant ruderal vegetation, such as *Geum urbanum*, *Chaerophyllum temulum* or *Chelidonium majus*.

Data processing and data analysis

We used a geographic information system (ArcMap of ArcGIS 10.3.1, ESRI, Redlands, California) to integrate the density distribution mappings of common ragweed as roadside line features to a digital form of the regional road network (OpenStreetMap and contributors, CC-BY-SA). In a second step, we split this network into 3-m-long spatial units resulting in 198,327 single road cells of 3 m length longitudinal to road direction. Each cell contained information about road type, traffic direction, roadside habitat and plant density for the seasons 2008, 2009, 2010, 2011 and 2012.

Road sections: To better understand how common ragweed interacts with variations in roadside habitats and traffic intensity within the road network at a regional scale, we split the entire network into 49 *road sections* based on existing junctions and t-junctions (a-road: *n* = 14, state road: *n* = 16, district road: *n* = 8, parish road: *n* = 11). We defined these sections as our main investigation units for analyses on temporal and spatial changes in the number of road cells colonized by common ragweed. Within

their boundaries, each of the units is homogeneous in relation to the type of corridor or traffic intensity.

Road cells: To get a deeper insight into the roadside population dynamics we used *road cells* as a second level unit within our main unit *road section* in the sense of a high-precision investigation of the interactions between traffic intensity and habitat feature at the local scale. As we wanted to uncover plant density variations individually for each *road cell*, we encoded the mapped plant densities (none, scattered, patchy, line-like, dominant) into numbers (0, 1, 2, 3, 4) and calculated the differences in population density between the years ($n = 4$ sub sets of *periods*, i.e. 2008/2009, 2009/2010, 2010/2011, 2011/2012). Each *road cell* now included information about plant density in the prior season, the difference between the two seasons (*change in population density*) and the plant density in the post season. To cover only those road cells where change in ragweed density could potentially be observed, we filtered the road cells so that either the prior season or the post season had to be non-zero.

Binomial generalized linear mixed model: To assess the effects of road type and year on the invaded portion of the road sections, we performed a binomial generalized linear mixed model ('glmer' from the r-package *lme4*) with the counts of invaded and uninvaded road cells in each section as a dichotomous response vector. We used *road type* (a-road, state road, district road, parish road) and *year* (2008, 2009, 2010, 2011, 2012) and their interaction as fixed effects and the nesting of *road sections* in *year* as a random factor.

Linear mixed-effects model: To unravel the effects of traffic and habitat on the dynamics of ragweed density, we used a linear mixed-effects model ('lmer' from the r-package *lme4*) with the categorical variables *roadside habitat* (disturbed, undisturbed, shaded) and *traffic intensity* (high traffic, low traffic) as fixed effects. As random effects we used again *road sections* nested in *year* to account for temporal and spatial nesting of the *road cells*. Here, *year* is used as a covariate and no longer as a fixed effect, as we were interested in the interactions between habitat feature and traffic intensity independently of annual dynamics. As response we used the *change in population density* based on the encoded population density categories (see paragraph on roadside cells). This vector ranged from "-4" (population in the *road cell* decreases from level '4' to '0' ['dominant' to 'uninvaded']) to "+4" (population in the *road cell* increases from level '0' to '4'). A vector value of "+1" for example would display an increase of plant density in the *road cell* by a whole factor level (e.g. 0 to 1, 1 to 2, 2 to 3, 3 to 4). This variable showed a normal distribution and hence a linear model was chosen.

Results

Traffic intensity and population expansion

As hypothesized, traffic intensity was related to the expansion of common ragweed populations within the road network. At the landscape scale, common ragweed colonized a portion of between 0.24 to 0.51 (a-road), 0.41 to 0.53 (state road), 0.29 to

0.35 (district road) and 0.46 to 0.36 (parish road) of all road cells in the respective corridor type between 2008 and 2012 (Fig. 3).

In the binomial generalized linear mixed model the *year* of investigation has the strongest effect on the number of colonized road cells while *road type* alone is not a significant predictor (Table 1). However, a significant interaction between year and road type indicates that the annual change in colonized roadsides differs significantly between road types. After the first year, we detected a system-wide strong increase of the mean colonization share (a-road = +0.19; state road = +0.09; district road = +0.12; parish road = +0.16). Beside this initial increase we found, for the remaining period, the lowest interannual variations along the a-road (+0.07 for 2009/2010, -0.02 for 2010/2011, +0.02 for 2011/2012) and the highest variations along the parish road (-0.08, -0.15, -0.03). Furthermore, the colonization share for the high traffic corridors a-road and state road remained stable after 2008, with only minor fluctuations. The colonization of road cells in the low traffic corridor types showed a different pattern, with a weak decreasing trend in the district roads, and a sharp drop in the parish roads (Fig. 3).

Habitat features, traffic intensity and population growth

Population density in already invaded road sections increased over the entire road network during the study but this process was strongly modulated by both traffic intensity and habitat type. Based on the linear-mixed model, both factors, *roadside habitat* and *traffic intensity*, significantly affect the mean change in population density of common ragweed in the road cells (Table 1). However, the most significant effect on change in population density is the interaction between *traffic intensity* and *roadside habitat* (Table 1), suggesting that some features related to the number of passing vehicles modulate the habitat effect within road corridors.

The interaction plot in Fig. 4 illustrates how the mean change in population density differed between the three habitat types *disturbed*, *undisturbed* and *shaded* in relation to the two traffic intensities. In general, there is a higher change in population density within high traffic corridors. While we found a lower change in density for undisturbed and shaded habitats compared to disturbed roadsides within low traffic corridors, the change was even higher in these habitats within high traffic corridors.

Table 1. Effects of a) Road type and year on the proportion of roadside cells colonized by *Ambrosia artemisiifolia* and b) Traffic intensity and roadside habitat on annual change in population density of *Ambrosia artemisiifolia* in 49 roadside sections.

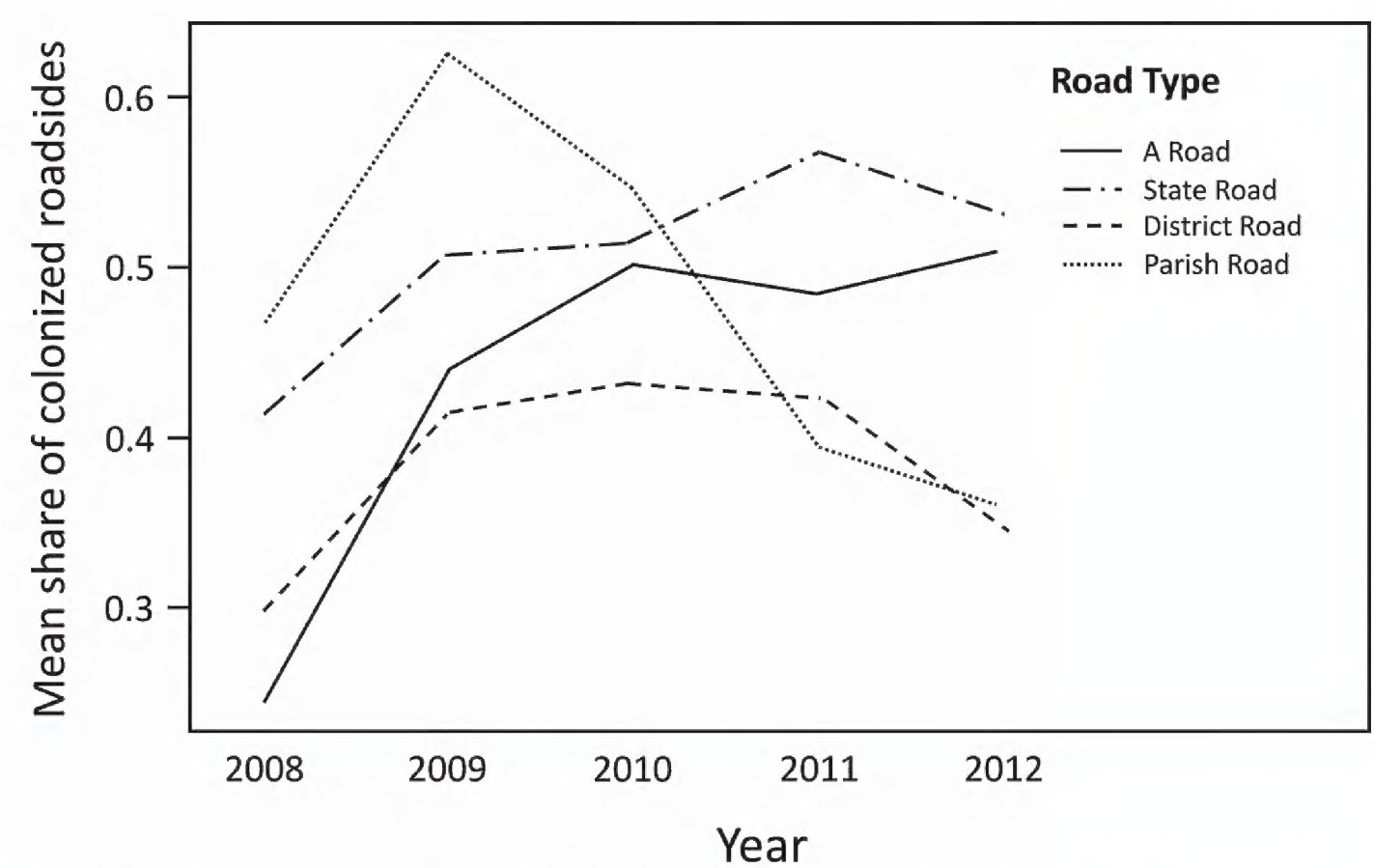| Model	χ^2	df	p
a) Colonized roadside cells (binomial glmm)			
Road Type	7.19	3	0.066
Year	14.68	4	0.0054
Road Type:Year	21.32	12	0.046
b) Annual Change in population density (linear mixed model)			
Traffic intensity	7.62	1	0.006
Roadside habitat	88.53	2	< 0.001
Traffic intensity:Roadside habitat	120.33	2	< 0.001

Figure 3. Proportion of roadsides in different types of road corridors, colonized by *Ambrosia artemisiifolia* in five years. Mean values are based on *road section* specific proportion of colonized *road cells* (n = 49 *road sections* in the road network).
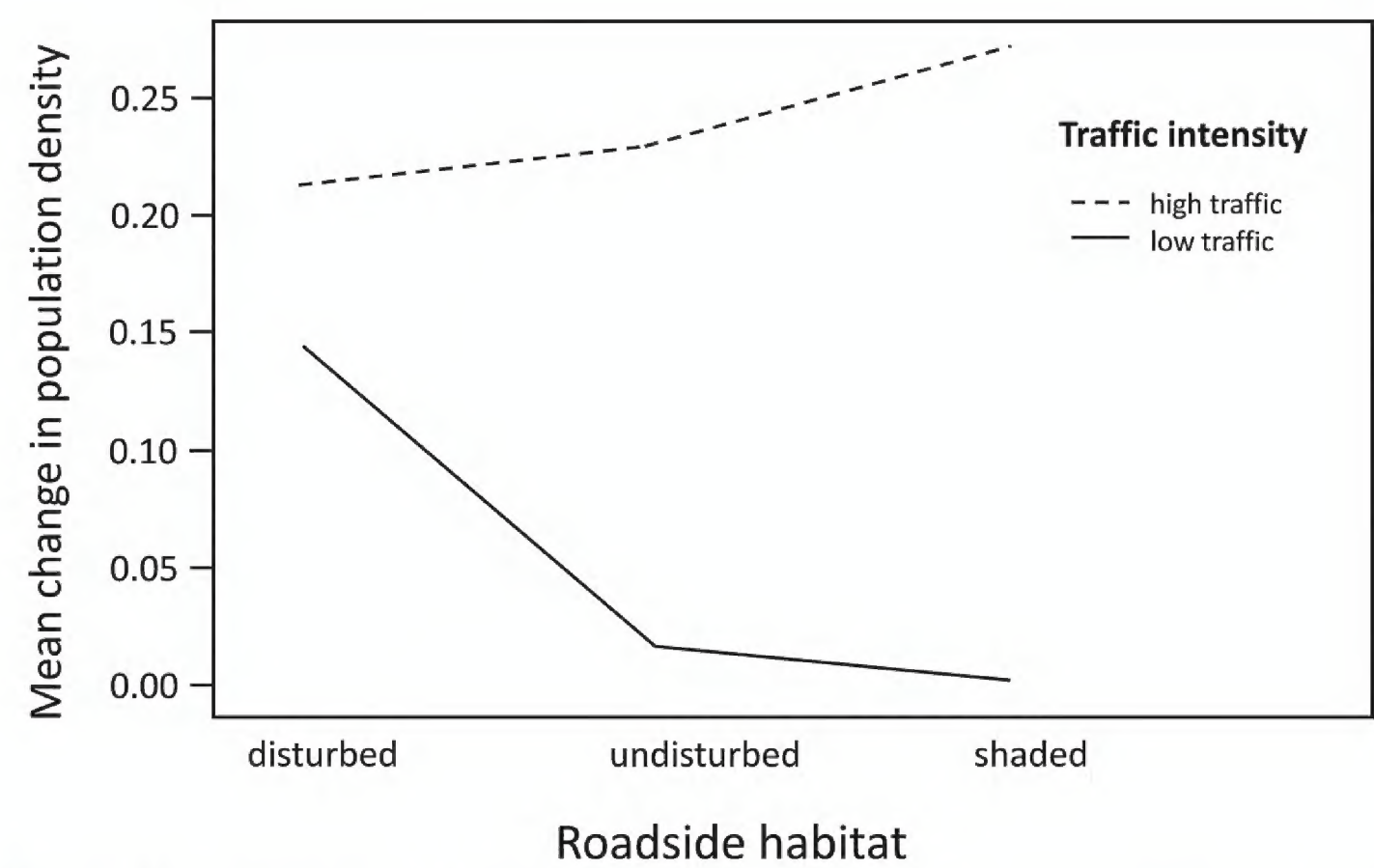

Figure 4. Mean change in population density of *Ambrosia artemisiifolia* between subsequent years in invaded road corridors with different traffic intensities. High traffic is merged from the corridor types a-road and state road, low traffic is merged from district road and parish road. Mean values are based on *road cell* specific population density categories (n = 303994 *road cells* in the road network).

Discussion

Plant invasions at higher spatial scales are shaped by highly complex dispersal pathways which interact with landscape characteristics (Pauchard and Shea 2006; Muthukrishnan et al. 2018). How such interactions modulate population growth in invasive species is a clearly understudied question. Here we show that the long-term dynamics in roadside populations in a common invasive species are shaped by an interplay of habitat features and traffic intensity. We found that a combination of high traffic intensity and high disturbance intensity of roadside habitats leads to high population growth in common ragweed. As a second insight, population growth in less suitable habitats with reduced availability of light and open soil, declines with reduced traffic intensity.

In general, a multitude of dispersal vectors shape plant dispersal in road networks (Kowarik and von der Lippe 2007; Auffret et al. 2014). The spread of common ragweed along roads, for example, is mainly fostered by agricultural machineries (Karrer 2014), soil movements, roadside maintenance and road traffic (Montagnani et al. 2017). Especially the two latter vectors promote plant invasions in road corridors by i) increasing the plant density in already existing plant patches and ii) supporting the colonization of empty patches – visible as a rapid range infilling at a regional scale (Warren et al. 2013; Rauschert et al. 2017). Rapid range expansions, on the other hand, rather depend on a high proportion of rare long distance dispersal events (LDD; Nathan et al. 2008). In the case of common ragweed, mainly agricultural machineries and contaminated soil transports are expected to support LDD events (Bullock et al. 2012; Essl et al. 2015) whereas mowing machines are supposed to act mainly at a regional scale ("medium dispersal"; Essl et al. 2015). A previous study demonstrated that road traffic modulates the population dynamics of ragweed at roadsides far beyond the reach of natural dispersal of the species, although the dispersal distances of the seeds are usually limited to the local scale (Lemke et al. 2019).

As a main insight from this study, traffic intensity seems to modulate the inter-annual variation of the spatial occupancy patterns of common ragweed within the regional road network. In the observation period 2009–2012, the percentage of colonized road cells was increasing or rather stable along high traffic roads (a-road, state road; Fig. 3). In contrast, the number of occupied road cells continuously decreased in the low-traffic parts of the road network during the same period (Fig. 3). This may be due to an interaction at the local scale. As illustrated in Fig. 4, disturbance and light availability are related to the colonization of roadside cells by common ragweed. Changes in these (or other) habitat features can lead to modified distribution patterns in roadside plants as shown by Dostálek et al. (2014). Increase in vegetation cover and shade limits the colonization success of common ragweed along roads (Fig. 4; Joly et al. 2011), while such change may favor other species. The perennial *Asclepias syriaca*, for example, preferably colonizes unpaved roadsides and those bordered by forests and grassland in Austria (Follak et al. 2018b)

The sudden increase in the overall occupancy of common ragweed in the road network after the first observation period (2008–2009, Fig. 3) seems to be a system-wide

event which might be related to interannual changes of the recruitment dynamics as well as to an unusually high seed production in the preceding year. Recruitment could have been fostered by the dry and warm summer of 2008 as these climatic conditions had visible negative effects on the competing roadside vegetation even in the following year while common ragweed is usually unaffected by warm and dry summers. Reduced competitive ability of the roadside vegetation is well known as a cause for increased recruitment success of common ragweed (Karrer and Milakovic 2016; Gentili et al. 2017). In the same vein, the warm summer could have fostered seed productivity in common ragweed, resulting in higher seed transport by all possible human mediated dispersal vectors in the system (e.g. by agricultural machinery, mowing machinery, vehicles and losses from soil transports).

Preferences for disturbed, open habitats correspond to the pioneer character of common ragweed (Montagnani et al. 2017). In contrast to many other pioneer plants, the spread of common ragweed is not facilitated by wind-dispersed seeds, pointing to human-mediated dispersal as key for the colonization of road networks (Essl et al. 2015). There are several possible vectors of human-mediated dispersal that could be related to traffic intensity. First, the number and speed of passing vehicles is positively related to direct dispersal by tires and the slipstream of cars and trucks (Lemke et al. 2019). Second, losses from trucks that carry soil or grain contaminated with seeds of common ragweed are a source for the establishment of new populations that is likely to increase with traffic intensity (Nawrath and Alberternst 2010). Third, the very relevant seed transport by mowing machinery (Vitalos and Karrer 2009) could indirectly be related to traffic intensity as different road types usually receive a slightly different maintenance by mowing. As our investigated road network receives the same frequency of mowing, seed dispersal by mowing machinery could still differ due to different types of mowing machines in the different road types. While all these traffic related dispersal vectors have been acknowledged as important agents in moving seeds of common ragweed, the interplay between traffic intensity and habitat features of roadsides – and its importance for population dynamics – has not yet been quantified at a regional scale.

Our linear mixed model revealed significant interactions between habitat features and traffic intensity and the population dynamics of common ragweed in the regional road network. However, the effect of habitat was considerably larger than that of traffic (Table 1). This may explain the declining plant density in low traffic road cells with less suitable habitat features (Fig. 4). Here, newly emerging populations are obviously more prone to local extinction due to interspecific competition (Patracchini et al. 2011; Gentili et al. 2017; Cardarelli et al. 2018; Lommen et al. 2018a) and a decreased plant performance (MacDonald 2009; Qin et al. 2012). However, disturbed low traffic road cells show a constantly high population growth in the observed road network. These results add evidence to previously demonstrated positive effects of disturbance on seedling recruitment and establishment on ruderal sites (Fumanal et al. 2008) and highlight the importance of disturbance events in road corridors as a driver for common ragweed invasions. Surprisingly, high traffic road cells displayed a consistently high population growth rate even in shaded and less disturbed road

sections. This trend can be attributed to the additional influx of diaspores due to traffic-mediated dispersal (Lemke et al. 2019) that obviously leads to the densification of populations even under less suitable habitat conditions. In the same vein, an increased propagule pressure from abundant roadside plant populations has been shown to partly compensate for seed traits that usually do not promote long-distance dispersal (von der Lippe and Kowarik 2012).

Bullock and colleagues (2018) propose to differentiate dispersal processes in spatial networks into "human-vectored dispersal" (HVD) and "human-altered dispersal" (HAD). Local impacts on population dynamics (e.g. by traffic-mediated dispersal) can thereby be identified as aspects of HVD. Still, the network-wide distribution of ragweed can be related to HAD as it is affected by the predominant land-use structures. A next step would be to concurrently analyze short-term and long-term changes in landscape patterns (e.g. temporary change in land use, construction works) in regard to spatiotemporal invasion patterns. While Christen and Matlack (2009) did not find any hints for a conduit function of roadside habitats, our study suggests that roadsides can function, depending on traffic intensity, either as habitat or as conduit for plant invasions. Roadsides with low traffic therefore offer only a habitat within the scope of natural population dynamics and thus limited dispersal functions whereas high traffic roadsides enable an increased population density for common ragweed with greater spread potential. The interaction between traffic-mediated seed dispersal and local habitat features is thus an important mechanism in understanding plant invasions in road networks at the landscape scale.

Conclusions

The drivers of roadside invasions by common ragweed are not yet fully understood, although there is increasing evidence of the separated effects of dispersal by traffic and road maintenance and habitat features (Vitalos and Karrer 2009; Bullock et al. 2012; Essl et al. 2015; Montagnani et al. 2017; Lommen et al. 2018b; Lemke et al. 2019). Our study adds further insights into these processes based on a detailed sampling of population data at a regional scale. As an innovation, we linked the assessment of dispersal vectors (traffic intensity) and habitat features (disturbance, shade) with population dynamics of common ragweed in a roadside network over a period of five years.

In our study, population growth of common ragweed proceeded even on roadsides with less suitable habitat conditions – but only along high-traffic roads. This indicates seed dispersal by vehicles and by road maintenance can compensate, at least partly, for less favorable habitat conditions. As a future direction, a threshold in traffic intensity and maintenance for a continued population growth along roadsides should be identified, based on more detailed data.

Our results on the interaction between traffic, roadside habitats and population dynamics have practical implications for habitat and population management to halt *Ambrosia* invasions along the road network. Depending on traffic intensity, colonized

roadsides can serve both as a stepping stone habitat and as conduit for common ragweed invasions in road networks as already indicated by Nawrath and Alberternst (2010) and Karrer et al. (2011). Management measures that aim at local eradication of *Ambrosia* populations should give priority to reducing the established roadside populations and their seed bank in critical parts of the road network. In the light of our results, most critical parts of the network with a high potential for traffic-mediated dispersal are high traffic roads with established populations and a high share of disturbed roadsides. This is in accordance with recommendations for prioritization of control measures along high-ranked roads in Austria (Karrer et al. 2011). For parts of the road network where the focus is on weakening and suppressing ragweed populations, an adjusted mowing regime is recommended, to prevent flowering and fruit set (Milakovic and Karrer 2016; Lommen et al. 2018b). Another way of containing the invasion is to establish a dense vegetation layer that impedes common ragweed germination and seedling establishment (Karrer and Milakovic 2016). Meanwhile our results indicate that shading, e.g. by tree plantations at roadsides, may not be sufficient in this respect, as dense traffic could partly compensate for the effect of shading on population growth. Measures should therefore aim at establishing a competitive herbaceous layer from appropriate seed mixtures that have been shown to effectively control *Ambrosia* establishment (Karrer and Milakovic 2016).

Acknowledgements

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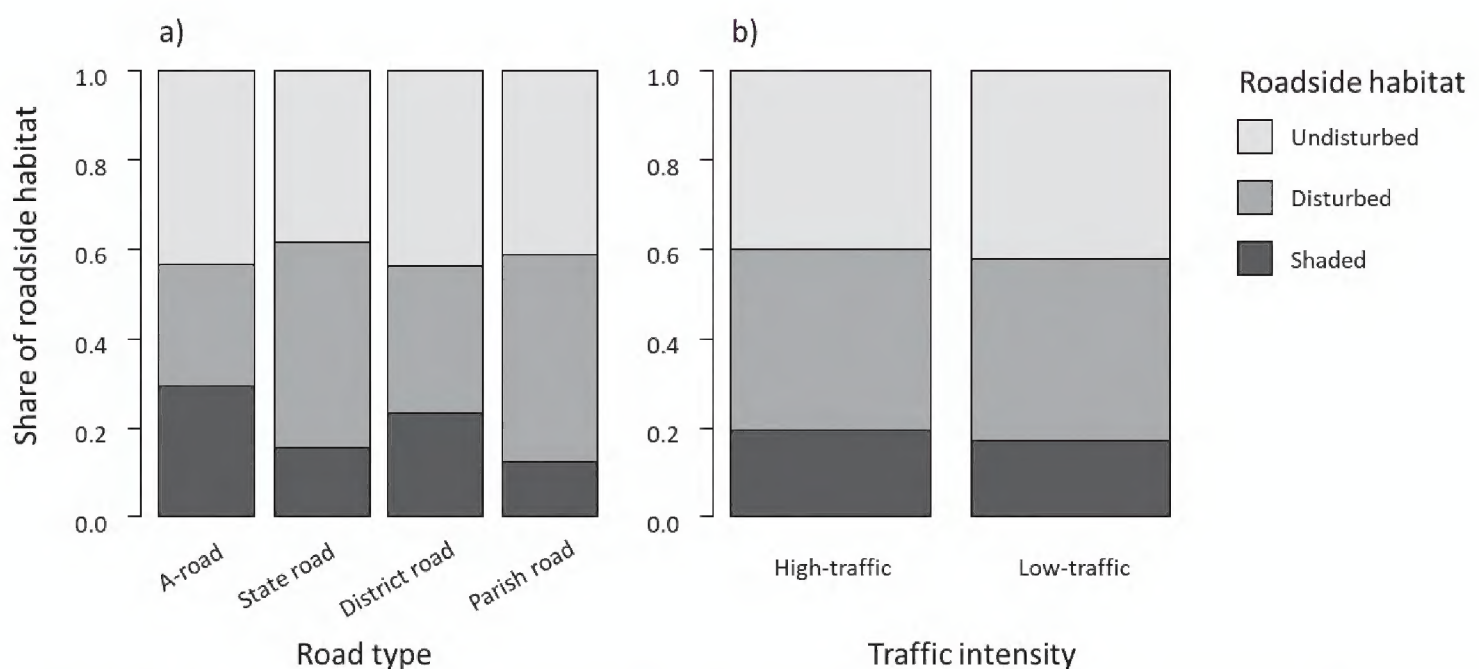
Appendix I

Figure AI11. Distribution of roadside habitat types within **a** road types **b** categories of traffic intensity over the entire road network.